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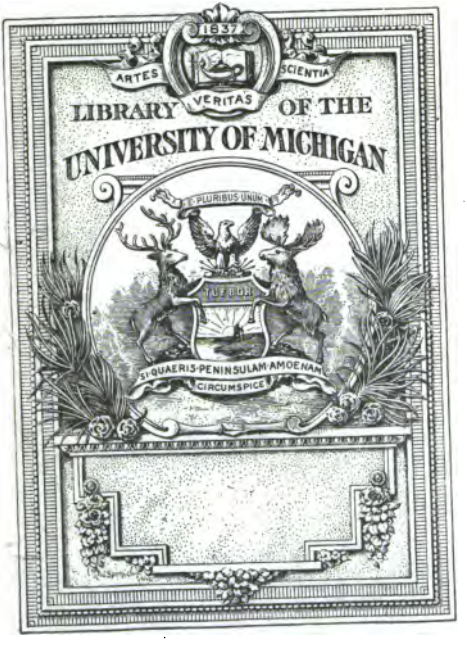
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MENDELISM

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MENDELISM

BY

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FELLOW OF GONVILLE AND CAIUS COLLEGE, CAMBRIDGE

SECOND EDITION

Cambridge

BOWES AND BOWES

1907

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PREFACE TO SECOND EDITION

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LESS than two years have passed since the first edition of this little book appeared, yet so rapid has been the progress of Mendelian studies that part of what was then written is already out of date. Why the dwarf pea sprung from tall ancestors breeds true to dwarfness: why the progeny of a black and a white rabbit are in one case all black, and in another all of the wild grey colour: why the 'pure' blue Andalusian fowl must ever remain a mongrel—these and other seeming paradoxes were clear two years ago. But why two white sweet peas should give a purple, and why two hairless stocks should revert to the hairy form—these were questions that were then unsolved. That experiment would give us the solution we were confident,

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and our confidence has been justified by the event. The sweet pea and the stock have yielded up their secret, and we are at last able to form a clear conception of the meaning of 'reversion.'

These recent discoveries have necessitated some re-writing and some additions. Mendel and his experiments stand where they always must stand, but the conception of synthesis has broken up, and the compound allelomorph is dead. Into their place comes the account of dihybridism in all its various aspects, and it is hoped that the diagrams added will assist the reader to grasp the unity which underlies this series of phenomena.

A short and popular essay like the present can give but little idea of the great body of facts already in existence. It would require a larger volume to do justice to the evidence, and to the devoted enthusiasm of the workers

who in three continents have sought it out. Those who are interested may be referred to the forthcoming book of Mr. Bateson on Mendel's principles of heredity.

Meanwhile the work goes on. Each new riddle solved propounds fresh riddles, and strengthens the hope of their solution. As year follows year, and experiment succeeds experiment, there is forced upon us a sense of what it all may come to signify for ourselves, of the tremendous powers of control that a knowledge of heredity implies. To-day we are only at the beginning. The prologue is nearing completion; the drama is yet to be written—and played.

R. C. P.

February 1907.

"His humour
Was nothing but mutation."

—*Cymbeline.*

Mendelism

It is the fortune of some great discoveries in natural knowledge to appear with the good will and acclamation of all. So it has been with gravitation and radio-activity. It is the lot of others to stir up immediate animosity, causing men to judge of them rather through their passions than by their reason. More especially is this so where the religious beliefs and prejudices of mankind are concerned, as instance Galileo and Darwin. In either case the issue of the forward step is from the first clear to all according to their degree. But it may at times happen that a discovery of the first magnitude excites but little interest or comment. For the meaning of it is not at once apparent. Such has been the fortune of Gregor Mendel's great discovery in heredity, of which the story forms one of

Introductory.

the most romantic chapters in the history of science. It is the aim of the following pages to give a brief account of Mendel's work with its more recent developments, and to touch upon some of the general consequences that flow from his experiments.

Biographical.

Gregor Mendel was born in 1822 of Austro-Silesian peasants. When twenty-one years of age he entered a religious foundation at Brünn, and a few years later was ordained priest. Subsequently he studied the natural sciences for several years in Vienna (1851—53). He became interested in the problems of hybridisation, and on his return to the cloister of Brünn commenced his classic experiments on the eating pea—*Pisum sativum*. The results appeared as a paper in the Proceedings of the Natural History Society of Brünn, under the title "Experiments in Plant Hybridisation." Besides this paper Mendel contributed very little to biological literature. Nevertheless, we now

know that he devoted much of his time to similar work on other plants. In a series of letters to Carl Nägeli, the botanist, he gives an account of his pea-experiments, and also of others dealing with *Lychnis*, thistles, etc. Nägeli, however, like the rest of his contemporaries who knew of Mendel's work, was unable to appreciate the magnitude of the discovery. Perhaps Darwin alone could have valued Mendel's little pamphlet at its proper worth, and into his hands unfortunately it never fell.

The Abbot of Brünn, for such he afterwards became, was a man of wide and varied interests. Besides his experiments on plants he is known to have carried out others on bees, though the record of them would appear to have been lost. Meteorology was a hobby with him, and he contributed numerous observations on the subject to the Brünn Natural History Society. He was also much interested in sun-spots, and was for a time the manager

of a bank. By the members of his cloister he was greatly liked and respected, though perhaps not altogether understood. He died of Bright's disease in 1884 at the age of 61.

Early neglect of Mendel's work.

For five-and-thirty years Mendel's work remained unknown. It had appeared at an unfavourable moment. Six years previously Darwin's views on the origin of species had been given to the world, and men of science were beginning eagerly to explore the new fields which he opened up. Hybridisers there had been before Darwin, but for lack of a central clue their results appeared as an inconclusive and disappointing tangle. Yet it was this very clue that Mendel's work supplied. With the advent of the "Origin of Species" men regarded as settled the question which the hybridisers had striven to answer, and directed their energies into other and more promising channels. Of late years doubts

have been cast upon the all-sufficiency of natural selection in the production of new species. A revival of interest in these matters, on the part of a few biologists, led in 1900 to the re-discovery of the principles of heredity which Mendel had clearly enunciated nearly forty years before. To gain an idea of the scope of these principles one cannot do better than turn to Mendel's own account of his experiments.

Mendel's Experiments.

In the selection of a plant for experiment Mendel recognised that two conditions must be fulfilled. In the first place the plant must possess differentiating characters, and secondly, the hybrids must be protected from the influence of foreign pollen during the flowering period. In *Pisum sativum* Mendel found an almost ideal plant to work with. The separate flowers are self-fertilising, whilst complications from insect-interference are practically non-existent. As is well known, there are numerous

varieties of the eating-pea exhibiting characters to which they breed true. In some varieties the seed colour is yellow, whilst in others it is green. In some varieties the seeds are round and smooth when ripe; in others they are wrinkled. Some peas have purple, others have pure white, flowers. Some peas again, when grown under ordinary conditions, attain to a height of 6 to 7 feet, whilst others are dwarfs which do not exceed 1½ to 2 feet. Mendel selected a certain number of such differentiating characters, and investigated their inheritance *separately for each character*. Thus in one series of experiments he concentrated his attention on the heights of the plants. Crosses were made between tall and dwarf varieties, which previous experience had shewn to come true to type with regard to these characters.* It mattered not which was the pollen-producing, and which the seed-bearing, plant. In every case the result was the

* See note at end, p. 82.

same. Tall plants resulted from the cross. For this reason Mendel applied the terms **dominant** and **recessive** to the tall and dwarf habits respectively. The next step was to collect the seeds thus formed, and to sow them in the following year. When this was done, it was found that both tall and dwarf plants appeared in the offspring. Each individual was either tall or dwarf, and no intermediate appeared. Thus in one series of experiments Mendel obtained 1064 plants, of which 787 were tall and 277 were dwarfs. That is to say, the tall plants were almost three times as numerous as the dwarfs. In other words, the dominant and recessive characters occur in the second generation of hybrids (F_2)* in the proportion of 3 : 1.

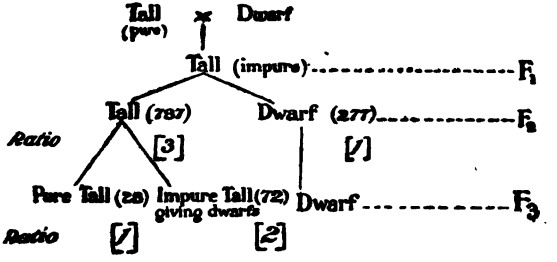
* For convenience it is customary to denote the hybrids arising from a first cross by the letter F_1 (= 1st filial generation). The successive generations arising from this F_1 generation are denoted by the letters F_2, F_3, ... etc. The parents of the F_1 generation are called P_1 (= 1st parental generation), the grandparents P_2, and so on.

In the following year the seeds of this generation (F_2) were sown as before. From the seeds of the dwarfs came only dwarfs, *i.e.*, the recessive character bred true. The tall plants, however, were not all of the same nature. Some of them produced seed which gave rise to tall plants only. Others, again, formed seed from which sprang both talls and dwarfs in the proportion of 3:1. The tall plants of the F_2 generation were of two kinds, viz., those which carried only the tall character, and those which carried both the tall and the dwarf characters. The former we may for the present call 'pure,' and the latter 'impure' dominants. Thus in one experiment plants were raised from the seeds of 100 tall plants of the F_2 generation. Of these 100 plants, 28 produced seed giving tall plants only, whilst 72 yielded seed which gave rise to both talls and dwarfs. Hence, of the 100 tall plants tested in the F_2 generation, 28 must have been pure for the tall

character, whilst 72 must have been carrying the dwarf as well as the tall character. The former numbers, 28 and 72, do not make a very exact approximation to the ratio 1:2. The numbers, however, are small, and the proportion is greatly affected by a slight deficiency on either side. From a much larger number of similar cases (between one and two thousand) Mendel found the ratio 1:2 borne out almost exactly. The dominants therefore which come in the F_2 generation are of two kinds—pure and impure. On the other hand, the dwarf recessives always breed true in whatever generation they appear. We may conveniently summarise the result of the experiments up to this stage in the following short table (p. 10).

By breeding subsequent generations Mendel shewed that the pure dominants and recessives always bred true, resembling in this way the original parents. The impure dominants, on the other hand, always gave

dominants and recessives in the constant proportion of 3:1. Since the pure dominants are only half as numerous as the impure



dominants, it follows that the impure dominant, on being selfed,* produces as offspring pure dominants, impure dominants, and recessives in the proportion of 1:2:1. And this held good for all impure dominants, no matter in what generation they were bred. We have considered the case of one pair of characters only, but Mendel shewed that the

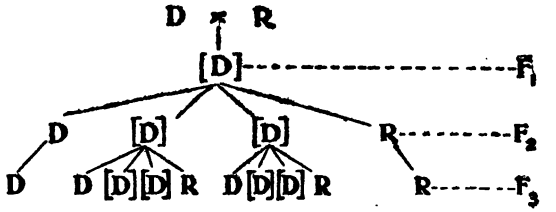
* See note at end, p. 82.

rule holds good for all the various pairs of differentiating characters studied by him. Wherever there occurs a pair of differentiating characters, of which one is dominant to the other, three possibilities exist:—there are recessives which always breed true to the recessive character: there are dominants which breed true to the dominant character, and are therefore pure: and thirdly, there are dominants which may be called impure, and which on self-fertilisation (or in-breeding where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter.

General Results of the Experiments.

We are in a position now to make a general scheme to shew the result of crossing individuals which each bear one of a pair of differentiating characters. If we denote the pure dominant by *D*, the impure dominant (which cannot be distinguished in appearance from the last) by [*D*], and the recessive

by *R*, we may construct the following scheme of inheritance.



Such a scheme brings out clearly the points already referred to. When two pure strains, each possessing one of a pair of differentiating characters, are crossed together, the resulting hybrids (F_1) all resemble the dominant parent.* When selfed, or bred among themselves, they give offspring (F_2), of which one quarter bear the recessive, and three quarters the dominant, character. Of the latter, however, only a third are pure dominants, giving, when selfed,

* The statement that the hybrid of the first generation cannot be distinguished from the dominant parent holds good for peas and many other forms of life, but, as will appear later (p. 29), it is not universally true.

offspring in which the dominant character alone appears. The remaining two-thirds are impure dominants, which on selfing behave as the original F_1 hybrids, and yield pure dominants, impure dominants, and recessives in the proportions 1:2:1. And this is true of all impure dominants, no matter in which generation they occur. Both the 'extracted' pure dominants and the 'extracted' recessives, which are formed in any generation after a cross, breed true to the types of the original parents used in that cross.

Mendel himself verified this principle of dominance for several characters in *Pisum*, finding round seeds dominant over wrinkled, coloured seed-coats over white seed-coats, yellow seed-colour over green, etc. Within the last few years the validity of the principle has been extended to numerous differentiating characters, both structural and physiological, in animals as well as plants.

Experiments subsequent to Mendel. (*a*) on Animals

To mention but a few cases: the coloured coat of mice and rabbits is dominant over the unpigmented or 'albino' coat; the long 'Angora' fur found in some rabbits is recessive to the normal short fur; the 'rose' comb which occurs in certain breeds of poultry, such as Hamburghs or Wyandottes, behaves as a simple dominant towards the high-serrated 'single' comb characteristic of Leghorns, Andalusians, and others.

(*b*) on Plants.

Owing to the numbers in which they can be produced, and the ease with which they can be controlled, plants lend themselves more readily than animals to investigations of this nature. Of the many characters already investigated a few only can be mentioned here. In wheat and barley the beardless have been shewn to be dominant over the bearded forms. The dwarf or 'Cupid' variety of sweet pea, but a few inches in height, behaves as a recessive to the normal form. In maize the yellow-

seeded variety is dominant over the white, and the so-called 'sugar' seed is recessive to the 'starch' seed. Among plants possessing coloured and white varieties of flowers it has been shewn that in general (*e.g. Datura*, stocks, sweet peas, etc.) the white forms are recessive to the coloured. The hybrid resulting from the crossing of pure white with a coloured form is always coloured, though its actual colour is not necessarily that of the coloured parent. Thus a picotee sweet pea crossed with a white may give, not picotee, but purple.

Waltzing Mice

The characters hitherto dwelt upon are concerned either with colour, or with what may be termed normal structural features. Leaving these we may turn for a moment to consider two most interesting cases, in which one of the pair of differentiating characters is in a markedly abnormal condition. Of the many breeds of fancy mice the Japanese 'waltzer'

is one of the most distinct, and derives its name from a curious habit of vigorously circling round, sometimes for hours together, as if intent upon its own evasive tail. It has been shewn that these mice suffer from a malformation of the labyrinth of the ear, and it is of the greatest interest to find that this condition behaves as a single recessive to the normal state.

The second case alluded to occurs in the sweet pea. Sometimes there may be seen a few plants in a row, which, though to all appearances healthy and vigorous, set little or no seed. The reason is at once apparent when a flower is pulled to pieces. The anthers are sterile, containing only a little degenerate pollen, and the flower is consequently incapable of the normal self-fertilisation which obtains among these plants. Such few pods as are formed, presumably owe their origin to insect agency, for the female parts of the flower are

Sterile Sweet Peas.

perfectly normal, and readily set seed when pollenated from another plant. The F_1 hybrids so formed are all normal, shewing that the fertile anther is dominant to the sterile. In the next generation (F_2) plants with sterile anthers reappear approximately in the proportion of 1:3 of the fertile, which is in accordance with expectation. This case of the sterile sweet pea is of great interest from its bearing on the problem of sex. Looked at from this standpoint we have here a unisexual form, a female, which has suddenly arisen from the normal hermaphrodite form by functional suppression of the male organs. It suggests that, in cases where the sexes are separate, this condition may have suddenly arisen from the hermaphrodite one. The story of sex, however, is too long and too complex for us to enter upon in this connection.

The characters we have just considered, though highly abnormal, are yet essentially

structural. The Mendelian principles of heredity have, however, been demonstrated in the case of other characters of a less tangible nature. It has been shewn, for instance, that the earlier ripening habit of Polish wheat is recessive to the later ripening habit of Rivett wheat. A still more interesting case occurs in the same species of plant. Certain forms of wheat are highly susceptible to the attacks of a fungus which causes 'rust,' whilst others are immune. It has recently been shewn that immunity in this instance behaves as a recessive to the non-immune condition. When an immune and a non-immune strain are crossed together, the resulting hybrids are all susceptible to 'rust.' On self-fertilisation such hybrids produce seed from which appear dominant 'rusty' and recessive immune plants in the expected ratio of 3:1. From this simple experiment the phrase 'resistance to disease' has acquired a more precise signifi-

Resistance to Disease.

cance, and the wide field of research opened up in this connection promises results of the utmost practical as well as theoretical importance. To the old question, "Who can bring a clean thing out of an unclean?" we are beginning to find an answer, nor is the answer the same as that once given by Job.

Theoretical Deductions.

So far we have been concerned with the phenomenon of dominance as enunciated by Mendel, and borne out by subsequent experiments. We must now consider the theoretical results which Mendel deduced from his facts. It is a matter of common knowledge, that in the majority of animals and plants the genesis of a new individual is the result of a sexual process, the essential feature of which consists in the union of a female cell, the egg or ovule, with a more minute male cell, the spermatozoon or pollen-grain. Such cells, both male and female, are termed **gametes**, and the cell formed by the fusion of a male with a female

gamete is spoken of as a **zygote**. This unicellular zygote, by a process of repeated nuclear division, ultimately gives rise to the adult animal (or plant as the case may be) with its contained germ-cells. The germ-cells, at first immature, subsequently ripen to form the gametes, thus completing the life-cycle. Since the gametes form the link connecting successive adult generations, the characters peculiar to the latter must be represented in the constitution of the former. In the case of a tall pea, some at least of the gametes formed, both male and female, must carry the tall character; for from an impure tall, three-quarters of the offspring are tall. And if the strain of tall peas is shewn by experiment to be pure for that character, all the gametes must be carrying that character, and that alone. The union of two gametes in this case will result in a zygote having the tall character, to the formation of which each gamete has equally contributed. Such a

zygote is known as a **homozygote**, and when it comes to form gametes, these will all be similar as regards the character under consideration. A zygote formed by the union of two dissimilar gametes—*e.g.*, in the case of peas, where one bears the tall, and the other the dwarf, character—is termed a **heterozygote.** The heterozygote frequently exhibits the form of the pure dominant, from which it can only be distinguished by the test of breeding. That the recessive character is likewise carried, is shewn by the fact, that when such heterozygotes are bred *inter se*, one quarter of the offspring produced are recessive. It is only in this way that we can distinguish between the pure tall pea, and the tall which bears the dwarf characters—between the pure 'rose' comb, and the 'rose' comb which carries also the 'single' comb. There are cases, however, in which the heterozygote does not resemble the dominant, but has a character

Homozygotes and Heterozygotes.

peculiar to itself. Reference will be made to such cases later on.

These facts led Mendel to the conception of pairs of unit-characters,* of which either can be carried to any one gamete to the exclusion of the other. A fundamental property of the gamete is that it can bear either one of such a pair of characters, though not both. But the heterozygote is formed by the union of two dissimilar gametes, and consequently the cells of the individual into which it grows must contain both characters. To reconcile these statements it must be supposed that at some cell division in the formation of gametes a primitive germ-cell divides into two dissimilar portions. Instead of the dominant and recessive constituents passing in combination to the two daughter-cells, the whole

Unit-Characters.

* Such pairs of unit-characters have since been termed **allelomorphic** pairs.

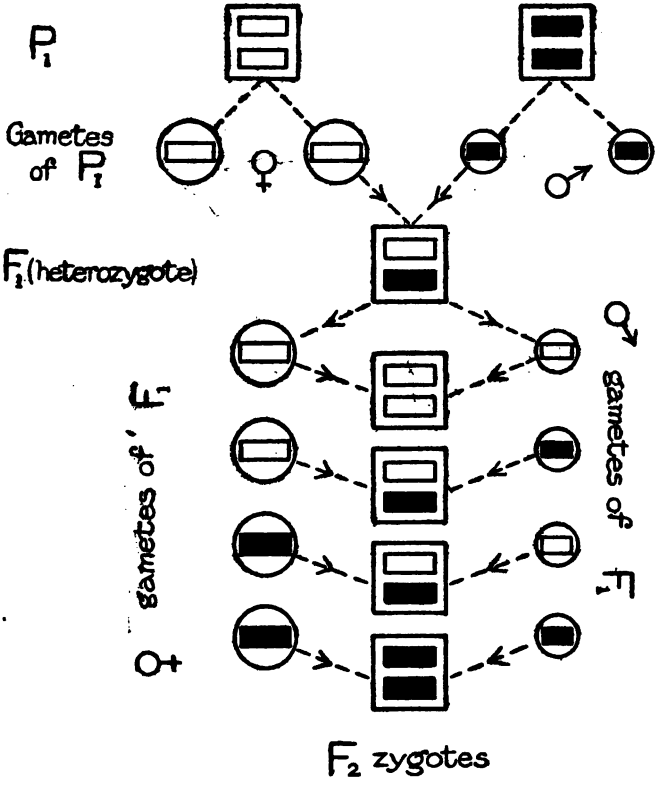
of the dominant goes into one of these, and the whole of the recessive into the other. From this it follows that every gamete contains only one of such a pair of characters, *i.e.*, it is *pure* for that character. In other words, a simple heterozygote, such as we are considering, *produces gametes of two kinds, and produces them in equal numbers.* The characters are said to **segregate** in the gametes. In this conception lies the simple explanation of the facts, that from the in-bred heterozygote come dominants and recessives in the proportion of 3 : 1, and that only one dominant in three is pure, the other two being heterozygotes.

The Principle of Gametic Segregation.

The argument may perhaps be rendered clearer by reference to the accompanying scheme. The zygotes are here represented by squares, and the gametes by circles. Every zygotic cell, being formed by the fusion of two gametes, is a double structure, and con-

tains two factors* belonging to any given pair of characters. In the scheme these factors are represented by small rectangles, those corresponding to the recessive character being shewn in black. The original parents (P_1) are supposed to be a pure tall and a pure dwarf, the latter being used as the pollen parent. All the ♀ gametes must therefore bear only the tall, and all the ♂ gametes only the dwarf, factor. Consequently only one type of plant can be formed in F_1, viz. a heterozygote containing the factors for both tallness and dwarfness. Owing to the complete dominance of the tall character these plants are indistinguishable from the tall parent. Since the factors are unsplittable, and since the gamete contains only half as many as the

* By this term it is convenient to denote the physical basis for the unit-character which exists in the gamete. Tallness in the pea is a unit character, and is transmitted from one generation to another by the 'tall' factor in the gamete.


P1
Gametes of P1
♀
♂
F1 (heterozygote)
♀ gametes of F1
♂ gametes of F1
F2 zygotes

zygote, it is obvious that when these plants produce gametes they must produce equal numbers of two sorts bearing the tall and dwarf factors respectively. Every ovule which bears the factor for tallness has an equal chance of being fertilised by a 'tall' or a 'dwarf' pollen-grain, and the 'tall' ovules will therefore give rise to equal numbers of homozygous and of heterozygous talls. Similarly the 'dwarf' ovules will give rise to equal numbers of heterozygous talls and of homozygous dwarfs. Hence, of every four zygotes in the F_2 generation, one will be homozygous for tallness, another homozygous for dwarfness, and the remaining two will be heterozygous in nature; though owing to the dominance of the tall character they will be indistinguishable in appearance from the pure talls. These we have already seen to be the proportions found by experiment, and the experimental results are to be regarded as the basis for the conception of unit-characters

represented in the gamete by unsplittable factors which segregate from one another during the formation of the gametes.

A convenient system of notation is to denote the heterozygote by the letters *DR*, thus signifying that it gives off equal numbers of gametes bearing the dominant and recessive characters. On the same system the pure dominant and the pure recessive are represented by the terms *DD* and *RR* respectively. So far we have considered only the results obtained by in-breeding the heterozygotes. The theory of gametic purity can be further tested by deducing from it the results which should follow from crossing the heterozygote with either of the homozygotes, and seeing how far such theoretical results accord with those obtained by experiment. When the heterozygote *DR* is crossed with the recessive *RR*, each dominant and each recessive gamete arising from the former

Homozygote bred with Heterozygote.

can unite only with a recessive gamete formed by the latter. Consequently we should look for the production of equal numbers of zygotes of the constitution *DR* and *RR*. This is what actually happens on crossing a fowl having a single comb (*RR*) with one having a heterozygous 'rose' comb (*DR*). Half the offspring are pure recessives, and the other half are dominants which may be all proved to carry the 'single' character, *i.e.*, are heterozygotes. Similarly, when the heterozygote *DR* is crossed with the pure dominant form *DD*, we should, from theory, expect all the offspring to be dominant in form, and one half of them to be pure dominant. Here again experiment has borne out theory. The generalisation known as the principle of gametic segregation may be regarded as firmly established on the phenomena exhibited by plants and animals, when strains are crossed which possess pairs of differentiating characters. Whether the principle applies

universally or not can only be answered by subsequent experiment.

We have already seen that the heterozygote frequently resembles the dominant homozygote so closely that the two cannot be distinguished by inspection alone. This is by no means always the case. It sometimes happens that the heterozygote, whilst bearing a general resemblance to the dominant, differs from it sufficiently to enable us to tell the two apart. The white Leghorn breed of poultry is characterised by its pure white plumage. In this case white plumage is dominant to coloured, but the dominance is not quite perfect. When a white and a brown Leghorn are crossed together, all the resulting offspring are white,* but almost

Limitations of the Phenomenon of Dominance.

* We know now that there also exist white chickens in which the whiteness behaves as a simple recessive to colour, and that these recessive whites are often indistinguishable in appearance from the dominant white. Not always does the plumage proclaim the fowl.

invariably have a few coloured feathers. The presence of these 'ticks' is the outward and visible sign of the heterozygous nature of the bird on which they occur. Such birds give off equal numbers of gametes bearing the white and coloured characters. This is easily tested by breeding them together. It is found that from such matings one quarter of the offspring are coloured recessives, whilst the remainder are pure white, or white with a few ticks. The heterozygote resembles the dominant form much more closely than it does the recessive. Though we may speak of dominance in such a case, it is necessary to remember the dominance is not perfect. This, however, makes no difference to the essential feature of Mendel's discovery, which is of course the segregation in the gametes of the factors corresponding to the dominant and recessive characters.

In addition to cases where the heterozygote differs slightly from the dominant

homozygote, there are others in which it is quite distinct from either parent, and exhibits characters peculiar to itself. The blue Andalusian fowl offers a very pretty instance of this. Breeders have long recognised the difficulty of obtaining a pure strain of this variety. No matter how carefully the blues are selected they always throw 'wasters' of two sorts, some pure black, and others of a peculiar white with black splashes. Careful breeding shews that, on the average, one half of the offspring from a pen of blue Andalusians come blue, one quarter black, and one quarter white. These proportions at once suggest that the blues are heterozygotes. For we have already seen that the breeding of heterozygotes together results in one half of the total offspring coming heterozygotes. If this is so, it follows that the blacks and splashed whites are by nature homozygous, and consequently ought to breed true. Ex-

The Case of the Andalusian Fowl.

periment has shewn that such is actually the case. Further, we should be led to expect heterozygous offspring from a union of the two different homozygotes. Here again the experimental result accords with the theory. When splashed black and white are bred together, all the offspring without exception are blue. Paradoxical as it may sound, the mating together of the black and the white 'wasters' gives a proportion of blue Andalusians twice as great as does the mating of blue with blue.* The black and the white splashed are really the pure breeds; the 'pure' blue Andalusian is, and from its nature ever must be, a mongrel. From our point of view it is of interest as a case

* The following scheme, which may be compared with that on p. 12, will perhaps serve to render the above account easier to follow. The theory of course supposes that the blues are giving off white-bearing and black-bearing gametes in equal numbers, there being no such thing as a blue-bearing gamete. In the cross blue × blue the ♀ is producing

where the appearance of the heterozygote is quite unlike that of either of the homozygotes from whose union it springs. Yet, though there is no dominant and no reces-

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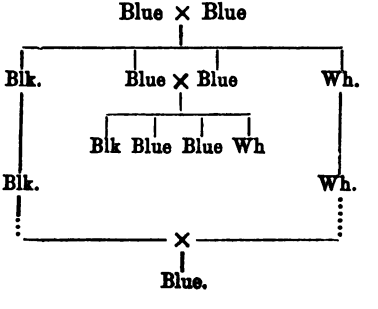
equal numbers ($2n$) of 'white' and 'black' eggs—the ♂ equal numbers of 'white' and 'black' sperms. A 'white' egg therefore has an equal chance of being fertilised by a 'white' or a 'black' sperm. When 'white' meets 'white' the result is white, and when 'black' meets 'black' the result is black. But when 'white' meets 'black' the result is blue. Hence $2n$ white eggs result in n white and n blue zygotes. Similarly, $2n$ 'black' eggs give rise to n black and n blue zygotes. Therefore if the blue ♀ produce $4n$ eggs to the blue ♂, n of these will result in black zygotes, n in white zygotes, and $2n$ in blue zygotes. In other words, the black, white, and blue birds produced must be numerically in the proportion of 1 : 1 : 2. And this is the proportion found by experiment.



sive here, the essential feature of gametic purity could not be shewn more clearly.

The cases which we have hitherto considered, concern only a single pair of differentiating characters, that is to say, are cases of **monohybridism.** Where the original parents differ in two pairs of characters, the case is termed one of **dihybridism.** Mendel himself worked out several such instances, and found that the separate pairs, though obeying the same law of inheritance, were transmitted entirely independently of one another. When, for example, a tall yellow-seeded pea was crossed with a dwarf green-seeded one, the F_1 plants all exhibited the dominant character of each pair, and were tall yellows. In the next generation appear, as usual, talls and dwarfs in the ratio of 3:1, and also yellows and greens in the same ratio. If we suppose that there are 16 plants, it is clear that 12 of these will be tall, and that the other 4 will be dwarf.

Dihybridism.

Now of every 4 talls, 3 will be yellows and the other green. Out of our 12 talls, therefore, 9 will be yellows and 3 will be green. Similarly, of the 4 dwarfs, 3 will be yellow and one will be green. Consequently, the F_2 generation arising from the cross will consist of 9 yellow talls, 3 green talls, 3 yellow dwarfs, and one dwarf green. In other words, there will be for every 16 plants a class of 9 shewing both dominants; two classes of 3 each shewing the dominant character of one pair and the recessive of the other; and one plant with both recessive characters. Mendel established by experiment that these were the proportions that actually occurred, a result which has been amply confirmed since his time for other plants as well as for animals. And the principle may be extended indefinitely for any number of pairs of characters.

In the particular case which we have just considered, one of the original parents was

homozygous for both the dominant, and the other for both the recessive, characters. Precisely the same result would have been attained had the original parents been a tall green and a dwarf yellow, instead of a tall yellow and a dwarf green. In either case the F_2 generation contains the two original parental types, and also two other combinations which we must regard as novelties. Where the two pairs of characters are as distinct as height and seed colour, the re-combination of characters which appears in the second generation is easy to follow. Sometimes, however, the reason of the appearance of a novelty is not at first sight so evident. The sweet pea known as the 'Painted Lady' is characterised by a bright pink standard and lighter wings. The colour here is due to the sap, and is dominant to the absence of such sap colour, in which case the flower is white. In the cream sweet pea there is no sap colour, the tint of the flower being

Novelties.

due to the presence of yellow-colouring matter in the small bodies known as chromoplasts. Yellow chromoplasts are recessive to colourless ones. When a Painted Lady is crossed with a cream, the F_1 plants are all Painted Ladies. In the F_2 generation four classes occur, viz., Painted Ladies, cream Painted Ladies, *whites*, and creams; and these four classes occur in the ratio 9:3:3:1. The proportion in which the four forms appear at once suggests the explanation of the case, which consists, of course, in being able to define the unit-characters involved. These must be—

(*a*) Red sap colour dominant to no sap colour;

(*b*) Colourless chromoplasts dominant to yellow.

The white, which appears as a novelty in 3 out of every 16 plants, is due to the combination of the character 'no sap colour' brought in by the cream with the character 'colourless chromoplasts' introduced by the Painted Lady. The apparent difficulty of the case, at first

sight, lies in the fact that both of the unit-characters concern the same thing, viz., the visible flower-colour.

A somewhat similar case in animals is presented by the behaviour of certain types of comb in fowls. Attention has already been drawn to two forms of comb found in different breeds of poultry, viz., to the high serrated 'single' comb characteristic of the Mediterranean races, such as the Leghorns and Andalusians, and to the flattened papillated 'rose' comb with its posterior pike that occurs in Wyandottes, White Dorkings, and others. As was mentioned above, the single and rose combs behave towards each other as simple recessive and dominant. A third type of comb is characteristic of the Indian game fowl. This, the so-called 'pea' comb, is a rather low structure, possessing three well marked ridges, of which the median is somewhat higher than the two lateral ones. Towards the single comb it

The Combs of Fowls.

behaves as a simple dominant. When, however, the rose and pea combs are crossed together, as for example by mating a White Dorking with an Indian game, an entirely new form of comb results. This is a broad flattened and somewhat corrugated structure, exhibiting neither the pike nor working of a rose comb, nor the three ridges of a pea. From its resemblance in shape to the half of a walnut, it may be called the 'walnut' comb. It occurs normally in a certain breed of fowls, the Malays. One of its peculiarities is that from certain portions of it grow out small bristle-like hairs. They occur on the posterior part of it, and often form a band running right across the comb at the junction of its posterior third with the remainder. The junction is usually marked also by a distinct transverse groove. The peculiar feathering of the comb is a feature not found in any of the other three types mentioned above. When these hybrid walnuts are bred together, four

types of comb appear in the next generation, viz., walnuts, roses, peas, and *singles*, in the approximate ratio of 9:3:3:1. Here again the explanation of the case is at once suggested by this ratio. The two pairs of unit-characters concerned are (1) *Rose* which is dominant to *no rose*, and (2) *Pea* which is dominant to *no pea*. Walnut is the form taken by the comb containing both of the dominant characters, and the single appears when the dominant of neither pair is present.

The case of the fowl's comb is of great interest, because it throws fresh light upon the relations subsisting between the two members of an allelomorphic pair. Hitherto we have considered each member of such a pair as a definite entity, of such nature that the two are of equal value and interchangeable with one another, but not with the members of other pairs. We have looked upon the tall pea as tall because the factor for

The Allelomorphic Pair.

tallness is present, and we have regarded the conversion of a tall into a dwarf as involving the removal of the tall factor and its replacement by the dwarf factor. If two peas differ from one another solely in the pair of characters—tallness and dwarfness—we must suppose that for the characters in which they resemble one another they must contain identical factors, and therefore the same number of factors. For the one pair of characters in which they differ they each contain a factor, but a different one. On this view, then, the total number of factors must be considered to be the same in each plant. So long as the cases of dihybridism studied involved two widely different pairs of characters, this view remained an adequate explanation of the facts. The case of the combs, however, presented a difficulty. It differed from previous cases, in that two pairs of characters both affected the same structure, the comb. Rose and pea are both dominant to single,

and we cannot distinguish the single which is recessive to pea from that which is recessive to rose. Strip off 'roseness' from a rose and single remains. Strip off 'peaness' from a pea and single is left. Single is to be regarded as a common condition underlying both rose and pea, and it may become rose or pea according as the factor for either of these characters is added. The rose and the pea, therefore, each contain a factor more than the single, and the walnut contains two factors more.

So also with the many simple Mendelian cases already mentioned. The tall pea is a dwarf to which has been added the factor for tallness. Were our methods nice enough to dissect out and remove this factor from the gametes of the tall, we must suppose that they would produce only dwarfs. For the operation would allow of the manifestation of the dwarf character, which is always underlying the tall, and forming as it were the

substructure necessary for the building of the tall.

The Presence and Absence hypothesis, as we may term this view, offers a ready explanation of one of the most widespread phenomena of heredity—the existence of characters in alternative parts. For there are but two relations into which the unsplittable unit-character can enter with the individual. It may be present, or it may be absent, and no third relation can be conceived. From this we are led to ask, whether the hypothesis can be brought into any simple relation with the phenomenon of dominance. Is dominance the outcome of the presence of the given factor, and recessiveness the condition implied by its absence? At present we can only say that such a point of view is not at variance with the great majority of the cases hitherto worked out. Whether the few instances which now seem contradictory will

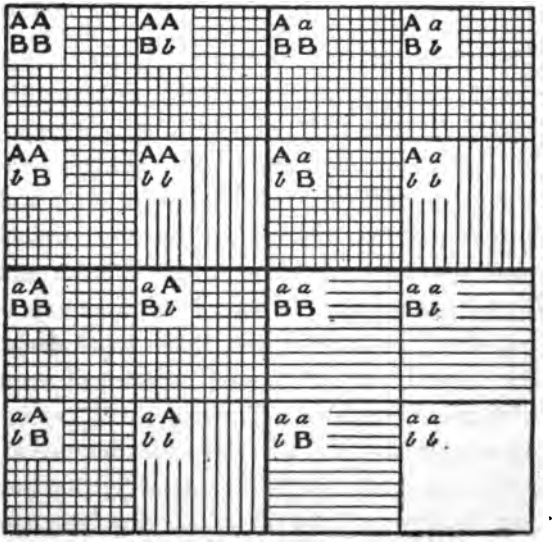
The Presence and Absence Hypothesis.

ultimately fall into line future work alone can decide.

Dihybridism again.

Returning now to the subject of dihybridism, we may briefly recapitulate in a generalised form the main features of the phenomenon before passing on to consider some special cases; and this may be conveniently done with the help of the diagram opposite. *Aa* and *Bb* denote two pairs of unit-characters, such that *A* is dominant to *a* and *B* to *b*. If we suppose one of the original parents to have been homozygous for *A* and *B*, and the other for *a* and *b*, we must represent them as *AABB* and *aabb* respectively. The constitution of the F_1 individual must therefore be *ABab*, and since it is heterozygous for the *Aa* pair it will give in F_2, $AA + 2Aa + aa$. This is denoted by the four large squares of the diagram. Again, since the F_1 individual is heterozygous for the *Bb* pair, the F_2 generation will be of the form

$BB + 2Bb + bb$ for this pair of characters. This is represented in the diagram by dividing up each of the 4 original squares into 4



again. Of the 16 squares resulting it will be noticed that:—

9 contain both *A* and *B*,
3 „ *A* but not *B*,
3 „ *B* but not *A*,
1 „ neither *A* nor *B*.

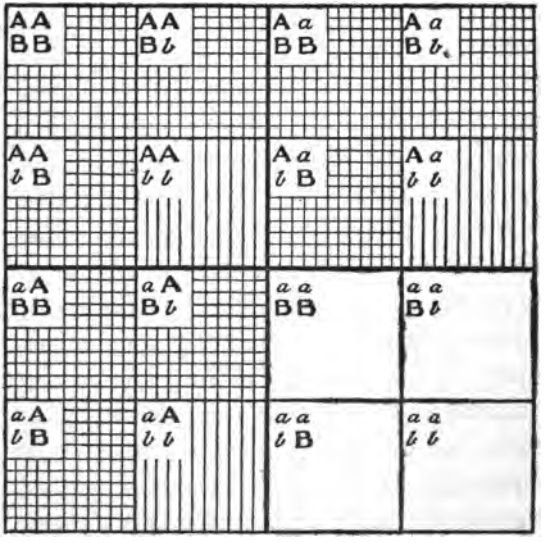
And this is the 9:3:3:1 ratio which we have already met with in several cases of dihybridism. Further, it may be pointed out that of the 16 zygotes only 4 are homozygous for both of the unit-characters contained. These are represented by the 4 squares on the diagonal starting at the left top corner of the diagram, and one of them belongs to each of the four classes represented in the 9:3:3:1 ratio. Hence, the chance of an F_2 zygote, which contains both dominants, breeding true is 1 in 9, and of an F_2 zygote containing one dominant is 1 in 3. The F_2 generation, in a case of dihybridism, consists of four types, viz. the original parents and two new ones. Of each of these four types a certain definite

proportion is fixed in this generation, and will afterwards breed true without any further selection. It is hardly necessary to point out the very great importance of this fact to those who are endeavouring to raise new and stable varieties by the method of cross-breeding.

Masked Characters.

Cases of dihybridism are known in which apparent complications are produced by the interactions between the two pairs of factors. Experiment has shewn that the wild grey colour in rabbits is dominant to black, and also that both grey and black are dominant to albino. When a rabbit of the wild grey colour is crossed with an albino, the offspring are all grey. On being bred together, these F_1 grey animals give in certain cases greys, blacks, and albinos in the proportion of $9:3:4$. The explanation is as follows. The two pairs of characters concerned are (1) pigmentation (A) dominant to absence of pigmentation or

albinism (*a*), and (2) greyness (*B*) dominant to blackness (*b*). The constitution of the F_2 family may be gathered from the accompanying diagram, which is constructed upon the same principle as that on p. 45. The



interaction of characters lies in the inability of colour, whether grey or black, to appear unless the pigmentation factor (*A*) is present. All individuals homozygous for (*a*) must be albino. Albinos carrying the grey factor (*B*) are constitutionally different from those in which that factor is absent. In appearance, however, the two classes are indistinguishable, and, moreover, any albinos bred together produce albinos alone. But as soon as the pigmentation factor is introduced by a suitable cross, the difference between the two classes of albinos is at once manifest. When crossed with a black, the albino homozygous for greyness (*aaBB*) gives only greys in F_1; that which is heterozygous (*aaBb*) gives equal numbers of greys and blacks, whilst the albino which is homozygous for blackness (*aabb*) gives nothing but blacks. The introduction of the pigmentation factor with the black parent brings about the development of the colour-factor which was all along resident in the

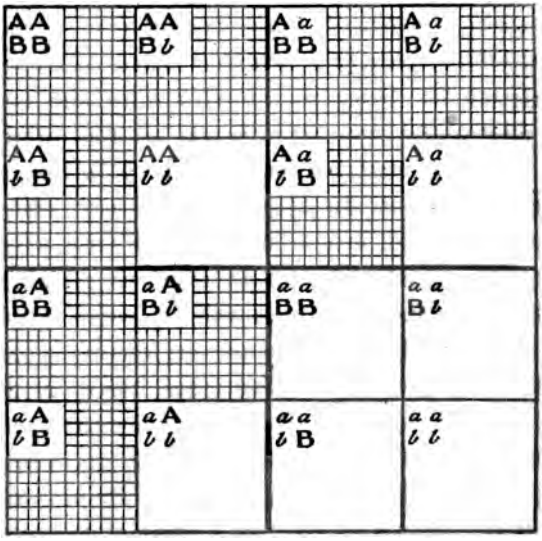
albino, but prevented from becoming visible, owing to the masking effect produced by the absence of pigmentation. The ordinary 9:3:3:1 ratio is converted into a 9:3:4 ratio, from the impossibility of separating the last two terms on external appearance. Appropriate breeding-tests reveal the fact that segregation of the grey and black factors goes on as usual beneath the mask of albinism.

An even more striking instance illustrating the interaction of factors is that of the sweet pea. All the white sweet peas at present known breed true to whiteness, yet in certain cases, when two whites are crossed, the hybrids are not white, but purple. Again, in other cases the hybrids may be Painted Ladies. The purple is in appearance identical with the form which is still found wild in Sicily, and the Painted Lady is also recorded by some old writers as a wild variety, though it is not known to

Sweet Peas.

occur as such at the present day. Both cases may be described as examples of reversion, and for the sake of simplicity we may confine ourselves to the case of the red. The explanation is clear. We are dealing with a case of dihybridism, in which each parent is homozygous for the presence of one of the two factors, and for the absence of the other. Colour is produced only when *both* factors are present in the zygote. Since each white parent brings in one factor, the hybrid must contain both, and must therefore be coloured. In the present case it will be red. If we represent the presence of one factor by A, and the presence of the other factor by B, a and b denoting their respective absence, we may make use of the scheme previously given (p. 45) for a case of simple dihybridism. Of the 16 squares in such a scheme there are 9 in which both A and B are present, and 7 in which either one or both of these is absent. Consequently, in the F_2 generation we should

obtain 9 reds and 7 whites out of every 16 plants. And this is what experiment has shewn to be actually the case. The 9:7



ratio is in reality a 9:3:3:1 ratio, in which, owing to interaction of the factors, we cannot

distinguish in appearance between the last three terms.

The case of the sweet pea throws a flood of light upon a widespread phenomenon which has long puzzled the naturalist—the phenomenon of reversion on crossing. To be red, or purple, the sweet pea must contain the two factors, without which it cannot manifest its colour. If either of these factors drops out from its constitution it must become white, and the white races of sweet pea have doubtless originated in some such manner. When a white pea lacking one of the two factors is crossed with a white lacking the other factor, the resulting zygote contains both the complementary factors necessary for the production of colour, and accordingly 'reverts' to the ancestral coloured form. So with the rabbit, where black and albino give only the wild grey. The black is a pigmented form lacking the factor for greyness, and the albino is

Reversion.

a grey lacking the factor for pigmentation. The cross brings together again the factors for pigmentation and greyness, and the hybrids are consequently coloured, reverting to the wild form. We may therefore define reversion here as "a simple and orderly phenomenon, due to the meeting of factors belonging to distinct though complementary allelomorphic pairs, which at some moment in the phylogeny of the varieties have each lost their complement."

But the reversion does not always occur in the first generation after a cross. The wild jungle fowl, from which the various domestic races are probably descended, has a single comb. We have already seen that when fowls with rose and pea combs are crossed, the F_2 generation consists of walnuts, roses, peas, and singles in the ratio 9 : 3 : 3 : 1. Rose and pea are to be regarded as each possessing a factor in addition to single, and the reversion is due to the meeting of the absence of these

two factors. Since in either case the presence of the factor is dominant to its absence, it is obvious that the reversion can only appear in the second generation.

The explanation of Darwin's famous case of the blue rock pigeon appearing in the second generation from a cross between a black barb with a white bird is probably similar. Blue underlies the blackness of the barb, but owing to the dominance of black it cannot become manifest, except in zygotes which do not contain the latter. And this can only happen in the second generation.

The re-combination of characters effected in dihybridism leads, as we have already seen, to the appearance of novelties in the second hybrid generation. Novelties are what the horticulturist wants, and here the new science of heredity has much to teach the practical man. Let us suppose that he has two varieties, each possessing a desirable character, and that he wishes to

Practical.

combine these characters in a third form. He must not be disappointed if he makes his cross, and finds that none of the hybrids approach the ideal which he has set before himself; for if he raises a further generation he will obtain the thing which he desires. He may, for example, possess tall green-seeded and dwarf yellow-seeded peas, and may wish to raise a strain of green dwarfs. He makes his cross—and nothing but tall yellows result. At first sight he would appear to be further than ever from his end, for the hybrids differ more from the plant at which he is aiming than did either of the original parents. Nevertheless, if he sow the seeds of these hybrids he may look forward with confidence to the appearance of the dwarf green. And owing to the recessive nature of both greenness and dwarfness, he can be certain that for further generations the dwarf greens thus produced will come true to type. The green dwarfs are all fixed as soon as they appear, and will throw

neither talls nor yellows. The less the hybrid resembles the form at which the breeder aims, the more likely is that form to breed true when it appears in the next generation.

But as all practical breeders know, the fixation of the required type is not always effected as simply as in the case of the green dwarf. Let us suppose that the parents are the same as before, and that the new form now required is a tall yellow-seeded pea. As we have already seen, the hybrids are all of the type required, viz., tall yellows. But they do not breed true. Still, the majority of their offspring (*i.e.*, nine-sixteenths), are tall yellows, and by saving the seed of these and growing further generations, using selection each time, the breeder expects eventually to fix the type. It is at this point that he frequently provides for himself a great deal of unnecessary labour, which a knowledge of Mendelian inheritance would spare him. These tall yellows all look alike to the eye; what, therefore, more natural

than to treat them alike, and to jumble up together the seeds collected from the different individual plants. Nevertheless, to do so is to court failure, or at best a tedious success. Out of every nine yellows, one, and one alone, is already fixed, whilst the remaining eight are, by their very nature, bound to throw other forms.* If the breeder saves the seed *from*

* How this comes about may be easily gathered by referring to the scheme on p. 45. Of the 9 zygotes containing both *A* and *B* (*i.e.*, the factors for tallness and yellowness), 4 are of the constitution *AaBb*, and will therefore give tall yellows, tall greens, dwarf yellows, and dwarf greens in the proportion 9 : 3 : 3 : 1; two are of the constitution *AABb*, and will give tall yellows and tall greens in the proportion 3 : 1; two are of the constitution *AaBB*, and will give tall yellows and dwarf yellows in the proportion 3 : 1; one alone is of the constitution *AABB*, and this will consequently breed true to both the tall and the yellow characters.

As an example of the practical working of these principles, we may briefly allude to the results obtained by Mr. Biffen, of the Agricultural Department of Cambridge University. Working on Mendelian lines Mr. Biffen has been able in a very few generations to build up and fix wheats combining the desirable characters of several varieties. Length of straw, cropping power, 'strength' of grain, immunity to

each plant separately, he will obtain what he wants, and will obtain it ready fixed. The idea that many generations are required for the fixation of a new variety is a wrong idea, and only arose because it was not unnaturally assumed that either plants or animals of identical appearance were also identical in their breeding qualities. To-day we realise that this is not necessarily the case, and Mendel's discovery has introduced principles which must largely modify the breeder's methods. For the points to be borne in mind are two. In the first place, all the possible forms which can emanate from a cross between two fixed strains appear in the second generation, provided that a sufficient number are grown; and in the second place, a certain

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rust—all these he has demonstrated to be unit-characters exhibiting Mendelian inheritance. Using this knowledge he has been able to produce pure strains of wheat which must greatly influence the agricultural outlook in this country when they come to be placed upon the market.

proportion of each of these forms is already fixed in the second generation. Two generations suffice to produce and fix the new variety, and one further generation is all that is required to indicate the fixed individuals.

Crossing for Vigour.

Again, since all the possible re-combinations of the characters involved in any cross come fixed in a definite proportion of the individuals of the second generation, it is obvious that the two original parental types will be among them. Now it is a well-known fact that in most cases a cross means increased vigour for the progeny. But the breeder is often shy of making such crosses, for fear of breaking up and losing the desirable combination of characters found in his original strains. Mendel's discovery may reassure him on this head. In three generations he can now reproduce the parental types, and reproduce them with all the increased vigour resulting from a cross.

Considerations such as these naturally lead us to ask, What is meant by the term 'pure-bred'? What is the criterion by which we are to judge the pure-bred thing? Until recently we should have said that this criterion was provided by the pedigree of the individual—that the individual was either more or less pure-bred for any given character, in so far as it could shew a longer or shorter line of ancestors possessing that character. To-day our criterion is an entirely different one. A plant or an animal is pure-bred for any given character when it has been produced by the union of two gametes each carrying that character. The single comb which arises from the union of walnuts, themselves the result of mating rose with pea, breeds as true as does the single of unblemished single ancestry. From a cross between a black and a white rabbit there come greys in the second generation, which breed as true to type as the

Purity of Breed.

wild rabbit of irreproachable pedigree. Pedigree is valuable as affording an indication of purity, but the pure-bred thing may, and often does, arise from a stock which is anything but pure. One thing may be pure-bred because of its ancestry, and in spite of its ancestry another may be equally pure. For the one and only arbiter of purity is the gamete.

Before dismissing the subject of dihybridism a brief allusion may be made to another phenomenon, from which important developments may be expected in the future. In the dihybrid cases hitherto considered, the two pairs of characters behave quite independently, in so far as the process of segregation was concerned. But in certain cases there occurs a form of coupling between the members of the different pairs. In the sweet pea, purple is dominant to red, and the erect standard is dominant to the 'hooded' standard. The sweet pea, which is heterozygous for both of

Coupling of Characters.

these pairs, is in appearance an erect purple, and if the case were one of simple dihybridism we should expect its offspring to consist of 9 erect purples, 3 hooded purples, 3 erect reds, and 1 hooded red. Actually, it consists of 2 erect purples, 1 hooded purple, and 1 erect red. And further experiment has shewn that, whilst the hooded purple and the erect red breed true, the erect purples always give both hoods and reds. In the F_2 generation the purples are to the reds, and the erects are to the hoods, as 3 : 1, but the hood is completely coupled with the purple, and in these strains is never found associated with the red.

In other cases it may happen that the coupling is not complete. Two forms of pollen grains occur in the sweet pea, viz. elongated and round, the former being dominant to the latter. In families where long and round pollen, as well as purple and red flowers, are found, the dominant is to the recessive as 3 : 1 for either pair. But instead of the purple

longs being three times as numerous as the purple rounds, there is actually but one purple round to about 12 purple longs. The deficiency of rounds among the purples is compensated for among the reds, where the rounds are to the longs in the ratio of about 3·3 : 1. There is coupling of longness with purple, and of roundness with red, but the coupling is not complete. Few cases of gametic coupling have been as yet worked out, and many points with regard to it are still obscure. Nevertheless, the phenomenon is of great scientific interest, and there is every probability that, as it becomes better known, it will be found of peculiar importance in the elucidation of the architecture of the gamete.

Such then are the facts elicited by Mendel and others, and such is the interpretation put upon them. Does all this, it may be asked, affect our conceptions of the nature and origin of living forms? The answer must be in

Mendel and current biological conceptions.

the affirmative. Of the fact of evolution we are certain. Of the workings of natural selection we have no doubt. But with regard to the nature of the variations upon which selection works there is much diversity of opinion. The discoveries associated with Mendel's name have introduced no fresh view here. Nevertheless, they must greatly influence our conception of the part played by the different forms of variation in the evolutionary process. To see why this is so will necessitate a brief historical digression. More than half-a-century ago Darwin recognised that the problem of the origin of species is inseparably bound up with the nature of variation. The evolution of fresh species depends upon the action of natural selection on the variations that occur in living forms. Individuals of a species, which from their variations are more adapted to their environment, survive in the struggle for

Variation and Natural Selection.

existence; individuals less adapted are placed at a disadvantage, and tend to perish in the competition with their more favoured kin. The survivors leave offspring, of which some shew the favoured variation in a rather greater, some in a rather less, degree. Natural selection sifts out the former as the parents of the next generation. And so for generation after generation. The process is a cumulative one. By the action of natural selection small variations are gradually worked up into a specific difference and finally fixed. Natural selection is, as it were, the guiding hand that is continually exerting a steady pressure upon the species, and the species, from its inherent variability, is a plastic thing, ever responding to the touch of natural selection. It is true that Darwin recognised that large variations may suddenly arise complete from the first, and he instances, among others, the cases of the large-crested Polish fowls, and of the familiar short-legged Ancon ram. But he

was disinclined to attach much importance to such variations in the production of species, holding that from the rarity of their occurrence they would rapidly become swamped by intercrossing with the normal form. He considered that it was by the action of natural selection on small continuous variations that species had been and were being built up. This idea, supported by the wealth of facts marshalled together by Darwin, dominated thought for forty years. Here and there a dissentient voice was heard, but it was not until ten years ago that Bateson drew attention to the frequency of Discontinuity in variation, and suggested that such saltatory variations may have played an important part in the production of species.

More recently the Dutch botanist, Hugo de Vries, has emphasised this point of view. He considers that the term 'variation' has been used to include several distinct phenomena. There are

Mutations.

variations which arise suddenly, and are discontinuous. These de Vries calls **mutations.** They are sharply divided from the stock whence they took their origin, and their inheritance is discontinuous. The mutation may be dominant to the original form, as for example the rose comb in fowls, which doubtless arose from the single. Or the mutation may be the recessive form, as in the Cupid variety of the sweet pea. The magnitude of the mutation may be great and striking, or it may be comparatively small. But whatever its size, its inheritance would seem to be according to the law of gametic segregation.

Another form of variability recognised by de Vries is found among the instances which he terms ever-sporting varieties.*

Ever-sporting Varieties.

The common snapdragon, *Antirrhinum majus*, is a case in

* A free translation of the original terms 'Halb-rassen' and 'Mittel-rassen.'

point. There exists a variety of this flower in which the yellow ground colour is relieved by red stripes. This striped variety apparently cannot be fixed. Among the plants raised from its seed there occurs a certain proportion, generally small, which produces red flowers. By selection it is possible to get a strain of snapdragons whose seed gives rise to over 90 per cent. of striped. Similarly, by selection of the red-flowered plants, a strain may be produced which gives about 80 per cent. of red, the rest being striped. In neither case did de Vries succeed in getting a pure strain, either of striped or of red. These ever-sporting varieties are undoubtedly complex in their nature, but as far as one can judge from his account, de Vries' experiments do not preclude the possibility of the existence of pure strains of striped and unstriped forms. It seems not impossible that when attention is more closely concentrated on the progeny of individual plants, a strain of reds may be pro-

duced which throws no striped, and possibly also a strain of striped which throws no reds. Segregation implies gametic purity, and before we can deny the presence of this phenomenon in the flower-colour of the snapdragon, further experimental work is necessary.

Lastly, we must recognise with de Vries the type of variation which he has termed 'fluctuating.' The occurrence of such fluctuations is universal. To say that no two individuals of a species are exactly alike is to reiterate a truism. The tall pea is a distinct race, and the dwarf pea is another. It is probable that the dwarf pea arose suddenly as a mutation from the tall. Having once arisen, it breeds true to the dwarf character. It is the property of a mutation to do so. But the dwarfs are not all of precisely the same height. Some are rather taller, and some rather shorter, than the normal. The dwarf mutation is subject to fluctuating variations which are probably

Fluctuating Variations.

due to the environment peculiar to each individual. A little more manure in its particular patch of soil, fewer surrounding weeds, greater freedom from the attacks of pests—these, and many other factors, may have contributed to the increased height of a plant as compared with its neighbours. But the fluctuating variations due to these causes are, so far as we know, not inherited. No horticulturist of experience would propose to produce from the dwarf pea a permanently taller race by a process of manuring. There is little doubt, but that the seeds from the richly manured, and those from the normally grown, plant would, when raised under similar conditions, each produce a row of plants indistinguishable in point of size. Nevertheless, the view is generally accepted, that careful selection of fluctuating variations will eventually lead to the improvement of a stock. At first sight this might appear to contradict what has been written above. Probably the

truth is, that under the head of fluctuating variations we are dealing with distinct phenomena. Doubtless some of the so-called fluctuations are in reality small mutations, whilst others are due to environmental influence. The difficulty of distinguishing between the two is very great. The simultaneous existence of small mutations and large fluctuations leads to the disguising of the former by the latter. Only careful and laborious analysis will avail us here, and such analysis is precisely what is at present lacking. The position is roughly as follows. Of the inheritance of mutations there is no doubt. Of the transmission of fluctuations there is no very strong evidence. It is therefore reasonable to regard the mutation as the main, if not the only, basis of evolution. And the great service which Mendel has rendered to this branch of philosophy is the demonstration of the fact, that the mutation, when once it has arisen, is not likely to be swamped by in-breeding with the

normal form, provided that it is not injurious to the species. We now recognise discontinuity in inheritance as well as in variation. The new character which arises as a mutation has its representative in the gamete. Once it has arisen, selection alone can eliminate it. Mendel's discovery, then, has led us to alter materially our ideas of the evolutionary process. The small fluctuating variations are not the material on which selection works. Such fluctuations are often due to conditions of the environment, to nutrition, correlation of organs, and the like. There is no indisputable evidence that they can be worked up and fixed as a specific character. Tall peas fluctuate considerably in height, but no gradual process of selecting the shortest will ever result in a permanent race of dwarfs. It is conceivable that the soil may be so doctored as to retard their growth, so that they come to mimic, as it were, the dwarfs. But remove the special conditions and their true

nature will be manifest. A cursory examination of horticultural literature must convince anyone, that it is by selection of mutations, often very small, that the gardener improves his varieties. Evolution takes place through the action of selection on these mutations. Where there are no mutations there can be no evolution. How and why these mutations arise is the great outstanding problem of biology. It is enough here to emphasise their existence, and to see how the recognition of them must modify current ideas.

The Conception of the Individual.

Our conception of the individual begins to take definite shape, and in place of the vague indefinable something by which we were content to mark off one individual from another, we have now a definite criterion in the unit-character. The individual is an aggregate of unit-characters, and individuality is the expression of a particular aggregation of such characters. Though often reacting upon

one another, the factors on which these characters are based behave as independent entities during the hereditary process, and heredity in consequence we may regard as a method of analysis, enabling us to judge of the number and condition of the unit-characters which go to make up the individual. The facts of heredity provide us with a series of reactions, which, if read aright, reveal to us the constitution of the living thing. And in the constitution of the living thing we have the key to its behaviour, to its potentialities and limitations, to what it can become, and what it can produce.

The position of the biologist of to-day is much the same as that of the chemist a century ago, when Dalton enunciated the law of constant proportions. In either case the keynote has been Discontinuity—discontinuity of the atom, and the discontinuity of the variations in living forms. With a clear perception of this principle, and after a long

and laborious period of analysis, the imposing superstructure of modern chemistry has been raised upon the foundation of the atom. Not otherwise may it be with biology; though here, perforce, the analytical process must be lengthier, both from the more complex nature of the material, and from the greater time involved in experiments on living forms. For unlike the chemist, the biologist is trammelled by the times and seasons. Nevertheless, the achievements of the last few years are such as to warrant us in looking forward hopefully to the time when our progress in the knowledge of the living may bear comparison, not unworthily, with the science of the things that are without life.

Economic Aspects of the Discovery.

Meanwhile, a few words on the general aspects of the conceptions that have arisen from Mendel's discovery may not be out of place in this connection. Economically their influence must be very great. Since

the principles of heredity form the very basis of the breeder's operations, anything which throws new light on these hitherto obscure matters must largely influence an important industry. From the little that has already been found out, the breeder is enabled to proceed with some degree of certainty. Till now his methods have been almost entirely empirical, and in great measure wasteful. He has bred together those that seemed likely to produce what he required. From their numerous offspring he has selected those few that seemed to come nearest to what he wanted. The rest, and these the great majority, must be rejected. Many be called, but few chosen. True, the end aimed at, fixation, is eventually attained. But its accomplishment entails much unnecessary waste by the way. Mendel's discovery must react strongly upon these methods. As soon as he recognises the definiteness of his problems; as soon as he realises the conception of unit-charac-

ters and their mode of inheritance—the breeder will reach his end more swiftly and more surely, with greater economy of time and of material. Few individuals, comparatively, will suffice for his preliminary process of analysis, and when this has been done, he may pass to greater numbers with a feeling of certainty as to the result. He will now know with what he is dealing. The possession of a transmissible character, desirable or otherwise, is no longer a question merely of degree. Either the individual has it, or has it not. Either it is represented in his gametes, or it is not. Once its presence or absence has been determined by analysis, the line can be definitely drawn. The breeder may proceed to build up synthetically, character by character, the plant or animal which he requires. His chief limitations will be those imposed by Nature upon the variations of living forms. These he will learn from simple observation and experiment, thereby saving time and labour in futile

attempts to achieve the impossible. For he will have read the riddle of the blue Andalusian fowl.

In conclusion, a few words upon another aspect of Mendel's discovery. How the discovery arose from the accurate analysis of a simple instance we have already seen. How the principle of gametic segregation applies to numerous cases in plants and animals has been pointed out. That it must apply to man also—the most complex of living forms—evidence already exists. If there is aught in these matters, the time is coming when they must be taken into account by those whose business is with the ruling and advising of their fellow-men; whose wish is to leave the world a little less aimless than they found it; who desire not "promiscuously to swim down the turbid stream and make up the grand confusion." Most of us are agreed that the circumstances of modern life are susceptible of change and of improve-

Conclusion.

ment. That end we seek to attain by better teaching and better sanitation. And in this direction we have made a start by concentrating attention upon the lower strata of society. Speaking broadly, our present policy aims at raising the standard of the less fit; at attempting to bring them closer by such means to those who are richer in natural endowment. Has such a line of endeavour any hope of permanent success? Or is it based upon a misconception of the nature of living things? Some there are, doubtless already, who question whether the general policy pursued with regard to the lowest classes of the nation is a sound policy; who are troubled with the suspicion that Hygiene and Education are fleeting palliatives at best, which, in postponing, but augment the difficulties they profess to solve. To them the facts of heredity may speak with no uncertain voice. Education is to man what manure is to the pea. The educated are in themselves

the better for it, but their experience will alter not one jot the irrevocable nature of their offspring. Permanent progress is a question of breeding rather than of pedagogics; a matter of gametes, not of training. As our knowledge of heredity clears, and the mists of superstition are dispelled, there grows upon us with ever-increasing and relentless force the conviction that the creature is not made but born.

NOTE

As some readers may possibly care to repeat Mendel's experiments for themselves, a few words on the methods used in crossing may not be superfluous. The flower of the pea with its standard, wings, and median keel is too familiar to need description. Like most flowers it is hermaphrodite. Both male and female organs occur on the same flower, and are covered by the keel. The anthers, ten in number, are arranged in a circle round the pistil. As soon as they are ripe they burst and shed their pollen on the style. The pollen tubes then penetrate the stigma, pass down the style, and eventually reach the ovules in the lower part of the pistil. Fertilisation occurs here. Each ovule which is reached by a pollen tube swells up and becomes a seed. At the same time the fused carpels enclosing the ovules enlarge to form the pod. When this, the normal mode of fertilisation, takes place, the flower is said to be **selfed.**

In crossing, it is necessary to emasculate a flower on the plant chosen to be the female parent. For

this purpose a young flower must be taken in which the anthers have not yet burst. The keel is depressed, and the stamens bearing the anthers are removed at their base by a pair of fine forceps. It will probably be found necessary to tear the keel slightly in order to do this. The pistil is then covered up again with the keel, and the flower is enclosed in a bag of waxed paper until the following day. The stigma is then again exposed and dusted with ripe pollen from a flower of the plant selected as the male parent. This done, the keel is replaced, and the flower again enclosed in its bag to protect it from the possible attentions of insects until it has set seed. The bag may be removed in about a week after fertilisation. It is perhaps hardly necessary to add that strict biological cleanliness must be exercised during the fertilising operations. This is readily attained by sterilising fingers and forceps with a little strong spirit before each operation, thereby ensuring the death of any foreign pollen grains which may be present.

The above method applies also to sweet peas, with these slight modifications. As the anthers ripen relatively sooner in this species, emasculation must be performed at a rather earlier stage. It is

generally safe to choose a bud about three parts grown. The interval between emasculation and fertilisation must be rather longer. Two to three days is generally sufficient. Further, the sweet pea is visited by the leaf-cutter bee, *Megachile*, which, unlike the honey bee, is able to depress the keel and gather pollen. If the presence of this insect is suspected, it is desirable to guard against the risk of admixture of foreign pollen by selecting for pollenating purposes a flower which has not quite opened. If the standard is not erected, it is unlikely to have been visited by *Megachile*. Lastly, it not infrequently happens that the little beetle *Meligethes* is found inside the keel. Such flowers should be rejected for crossing purposes.

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